Physiological Development Time and Zero Development Temperature of the Codling Moth (Lepidoptera: Tortricidae)

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ABSTRACT The physiological development time was determined for the immature stages of summer form codling moth, *Cydia pomonella* (L.), when reared at both constant and field-simulated temperatures. The phenological data thus obtained was used to examine the zero temperature threshold to model codling moth development. Two procedures were used to determine the base or zero development temperature for codling moth. They were the *x*-intercept, i.e., an extrapolation of the best-fit linear approximation of the reciprocal of time for development (days or hours) at each of a series of constant temperatures; and second using thermal units, i.e., physiological development time (degree-hours). The thermal unit was a constant at any logical rearing temperature when using the correct base (zero development) temperature. Physiological development time became increasingly curvilinear as the base temperature deviated from the correct value. Errors in base temperature, particularly at lower temperatures, introduce large errors into phenology models, reducing their reliability when used to time pest management procedures. Thermal units may be used to directly determine the base temperature or to validate the precision of the *x*-intercept. When reared at constant temperature, mean development time was 2,100, 6,100, and 5,800 degree-hours, but when reared under field-simulated (variable) temperatures the mean development time was reduced by 0, 500, and 1,100 degree-hours for eggs, larvae, and pupae, respectively. Development was retarded at 35°C when reared at constant temperature, but not when reared at field-simulated temperatures that were as high as 35°C for a few hours each day. There was no evidence for an upper temperature threshold using field-simulated temperatures. Modeling codling moth development in the field using field-simulated temperature data more accurately represents true development time. Fifteen percent of the larvae reared under long-daylength at 14.8°C entered diapause; whereas, there was no diapause at higher temperatures. Diapause induction at low temperature under long-daylength has not been previously reported.

KEY WORDS codling moth, degree-hours, development thresholds, physiological development, development rate, low temperature threshold

THE RATE OF development of *Cydia pomonella* (L.) is basically governed by environmental temperature (Rock and Shaffer 1983), and is measured more precisely by physiological time (degree-hours or degree-days) than by calendar time (days) (Taylor 1981; Tauber et al. 1986). Phenology models, using physiological time data, have been developed for codling moth to predict emergence of adults from the overwintering generation, eclosion of eggs, larval and pupal development, and generation time (Falcon and Pickel 1976; Falcon et al. 1976; Geier and Briese 1978; Riedl and Croft 1978; Jorgensen et al. 1979; Brunner et al. 1982; Richardson et al. 1982; Rock and Shaffer 1983). These models, all based on a linear relationship between temperature and rate of development, have been used with varying degrees of success (Rock and Shaffer 1983) to time spraying to control codling moth. Models using curvilinear functions have also been proposed (Shaffer and Gold 1985), but they are more complex than linear models and have not been routinely used. Although the assumption of linearity was not true for low and high-end temperatures, it has been assumed that those temperatures occurred so seldom that they could be ignored. Considering our experience with phenology models for codling moth, low and high temperature effects cannot be ignored. Others found that linear phenology models inaccurately simulate development at high temperatures (Shaffer and Gold 1985).

Our objective of this study was to investigate the phenology of codling moth development based on physiological time at both constant and field-simulated temperatures. These data then could be used to determine base temperature and to validate the accuracy of the base temperature determined by using the *x*-intercept method.

Materials and Methods

Rearings were conducted in custom-made controlled temperature chambers (0.3 by 0.3 by 0.3 m), using Love model 49 proportioning temperature controllers accurate to ±0.2°C (Love Instrument Co.,

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Wheeling, IL). All chambers were illuminated with two 35-W fluorescent lamps shinning through the Plexiglas cage door under a photoperiod of 17:7 (L:D) h. Humidity, as in the field, was not controlled and varied inversely with temperature, ranging from 80 to 30%, as one would expect over a range of temperatures from 13.9 to 35°C.

Temperatures in each chamber were monitored by a temperature integrator with a thermocouple sensor (Campbell A104T integrator, Campbell Instrument, Logan, UT) or a degree-hour meter (Pro-Temp700, Pro El Co., Salt Lake City, UT) and a maximum-minimum thermometer. Temperature integrators and degree-hour meters monitor the temperature continuously, measuring all temperature fluctuations within the cabinets, and producing actual degree-hour accumulations (Pruess 1983). Therefore, in this article the constant temperatures given were the mean temperatures recorded, but the degree-hours were the sums of the actual temperatures accurate to ±2%, the sensitivity of the degree-hour meters. Thermistor sensors were placed at several shaded locations inside the canopy of an apple tree in our orchard adjacent to the laboratory. The thermisters were interfaced with an Apple Computer (Apple Computer, Cupertino, CA) that controlled the temperature settings in the growth chambers, duplicating real time air temperatures. In nature, temperatures the eggs and larvae experience are not equivalent to air temperature. Leaf temperature lags ≈1–2°C behind air during early morning hours, parallels air temperature until noon, exceeds air temperature 1–2°C until late afternoon, and again parallels air temperature through the night. Fruit core temperatures from about midnight until sun-up generally parallel air temperature, lags 2–3°C behind air temperature from sun-up to near noon, and exceeds air temperature 3–6°C from noon until near midnight (J.F.H., unpublished data).

Codling moths used in the study were F_6–F_9 descendants of larvae collected at Wapato, WA. This colony was reared on green apples 2–3 cm diameter using the procedures of Hamilton and Hathaway (1966). Fluted fiberboard strips, within which the larvae had cocooned, were removed and placed into emergence cages within the growth chambers. Once every 24 h any emerged moths were removed to screen oviposition cages (45 by 45 by 42 cm). Sheets of waxed paper (31 by 35 cm) were crumpled and flattened, then hung on the inside walls of the cages to serve as oviposition substrate.

Egg Development. Physiological development time for eggs was determined using F_6 stock. Three replicates, with 92–244 eggs each <8 h old (on waxed paper in cylindrical fiberboard cages [8.5 by 17.0 cm]) were incubated at each of the following constant temperatures: 13.9, 20.1, 25.5, 29.6, and 34.4°C (one replicate at 14.8°C) and at field-simulated temperatures, with a low of 10°C and a high of 34.4°C. All eggs were checked at 8-h intervals for eclosion and heat units accumulated.

Larval Development. Physiological development time for larvae was determined with F_9 laboratory reared neonate larvae. Larvae <8 h old were placed singly on an immature apple near a needle puncture in the apple's epidermis. The needle punctures provided easy larval access into the fruit, which reduced larval mortality. Apples were held in stainless steel hotel trays (30 by 50 by 6.3 cm) covered with muslin cloth lids. One hundred larvae were reared at each of the following temperatures: 14.8, 20.1, 25.5, 29.6, and 35.0°C. Also, they were reared at field-simulated temperatures. The relative humidity was uncontrolled but was of no significance except before the larvae entered the fruit. Fluted fiberboard strips were placed in the trays to serve as cocooning–pupation sites. Larval maturation was considered complete when they began spinning their cocoons. Trays were inspected for cocoons every 8 h. The flutes with cocoons were removed to another growth chamber, and the heat units since hatch were recorded.

Pupal Development. Cocoons of the above larvae <8 h old were caged individually in 2-dram (7-ml) stoppered clear glass vials and held at 14.8, 20.1, 25.5, 29.6, and 35.0°C—also at field-simulated temperatures. Vials were checked at 8-h intervals, all emerged moths collected, and the accumulated heat units since cocooning were recorded. After 7 mo, all cocoons from which adults had not emerged were opened to determine the insect's status (i.e., in diapause or dead).

Degree-Hours. The degree-hours required for development of each life stage was read directly from the degree-hour meters, which was a record of actual temperatures in the cabinets. Campbell temperature integrators were used to obtain actual and mean temperature per cabinet. The development times measured were oviposition to hatch, hatch to cocooning (larval development time), and cocoon to adult emergence (pupal development time).

Base Temperature Determination. Base temperatures were determined using the x-intercept method, i.e., by regressing rate of development ($1/d_i$ where d_i = calendar time for development) versus temperature and extrapolating the regression line to the x-intercept. Base temperatures were also determined by comparing the number of thermal units (TU) for development. Thermal units were determined using the equation

$$TU = d_i\,(t_i - b), \qquad [1]$$

where d_i = development time in hours, t_i = temperature at which the insects were reared, and b = the base temperature (Arnold 1959, VanKirk and Aliniazee 1981). By substitution, the correct b would give the same number of thermal units at each temperature, as long as the rearing temperatures used were between the lower and upper temperature thresholds. The thermal unit sums would not be a constant, but different at each temperature, if the base temperature was incorrect. The assumption was that temperature was the only rate controlling factor, which is generally true for many insects (Liu et al. 1995).

Data were analyzed by linear regression (Steel and Torrie 1960, Draper and Smith 1966). The lack-of-fit test was by Draper and Smith (1966). Significant dif-

Table 1. Physiological development time in degree-hours centigrade (°h) at constant or field-simulated temperatures for summer form codling moth eggs in Yakima, WA

Temp. °C	No. eggs	Min. no. °h	Max. no. °h	Mean no. °h	Mean no. days	95% CL	% hatch
Constant							
13.9	420	1,872	2,434	2,126b	22.7	2,112–2,141	59.1bc
14.8	140	1,920	2,360	2,067ab	17.7	2,053–2,080	84.3a
20.1	408	1,866	2,459	2,135b	8.7	2,124–2,144	74.3ab
25.5	420	1,848	2,340	1,984a	5.3	1,970–1,997	49.5bc
29.6	278	1,906	2,400	2,028a	4.4	2,007–2,049	37.1c
Field-simulated	406	1,839	2,405	2,089a	10.7	2,067–2,112	66.0ab

Values with common letters within a column were not significantly different at $P \leq 0.05$. (Fisher LSD multiple comparison test).

ferences were determined using Fisher least significant difference (LSD) multiple range test at the 0.05 probability level (Hintze 1997).

Results

Egg Development. Heat units required for development of eggs are given for all rearing temperatures, except 34.4°C where only four eggs survived to hatch (Table 1). Mean development time was 2,071 ± 87 degree-hours centigrade. The ±87 degree-hours equals 7.25 h at 22°C, which corresponded to the 8-h spread in egg collections. Mortality of the eggs increased as the temperature increased from 14.8 to 34.4°C; at the latter temperature, mortality was 99.5%. Highest percentage hatch was at 14.8°C (Table 1). Field simulated temperatures, where temperatures were at or somewhat above 34.4°C for a few hours each day, did not change the physiological development time or induce a high egg mortality. Apparently, 34.4°C was deleterious only when eggs were reared continuously at this temperature.

Larval Development. Physiological development times for larvae (Table 2) were similar at 14.8, 20.1, and 25.5°C, but significantly longer at 29.6 and 35.0°C. Mortality was highest at 35.0°C (Table 2). The field-simulated temperatures produced the shortest development time (Table 2), but not significantly different when the two upper temperatures were excluded from the data set. Using the non-overlapping confidence limit statistic, development at field-simulated temperature was significantly different from all other temperatures (Table 2).

Pupal Development. Physiological development times for pupae were similar at all constant temperatures tested except 35.0°C, where there was 100% mortality (Table 3). Development time was significantly shorter for field-simulated temperatures. Reduced emergence at 14.8°C resulted in part, because some larvae had entered diapause (15%).

Development by Males and Females. Differences in physiological development times for males and females were not statistically significant (Table 4).

Base Temperature Determination. Rate of development, $1/d_i$, was calculated using linear regression for eggs (Fig. 1A), larvae (Fig. 1B) and pupae (Fig. 1C). The regression lines were extrapolated to the x-axis and the x-intercept represented the base (or zero) development temperature for each stage. For eggs, mean development rates were linear between 13.8 and 29.6°C. Only 4% of the eggs survived at 34.4°C. The x-intercept was the same whether including or excluding 34.4°C because there were so few data at that temperature (Fig. 1A). A lack-of-fit test for linearity for egg development, with the high temperature data, was significant ($F = 70.7$; df = 4, 978; $P \leq 0.05$), indicating that the data points deviated significantly from linearity. By extrapolation, the x-intercept for eggs was at 10.4°C (Fig. 1A).

The rates of development for larvae at temperatures of 14.8, 20.1, and 25.5°C were linearly related (lack-of-fit $F = 2.68$; df = 1, 212; $P \leq 0.05$); but not when the 29.6 and 35.0°C data were included ($F = 20.1$; df = 2, 270; $P \leq 0.05$). The x-intercept for those points having a linear relationship was 10.3°C (Fig. 1B). The x-intercept with all five temperatures included was at 6.9°C; with the four lower temperatures it was at 9.0°C (Fig. 1B). The thermal unit comparison indicated that 6.9°C was definitely an incorrect base temperature.

Table 2. Physiological development times in degree-hours centigrade (°h) at constant or field-simulated temperatures for summer form codling moth larvae in Yakima, WA

Temp. °C	No. larvae	Min. no. °h	Max. no. °h	Mean no. °h	Mean no. days	95% CL	% cocooning
Constant							
14.8	100	4,762	9,869	6,136a	53.3	5,892–6,379	62
20.1	100	4,767	15,595	6,349a	26.3	6,038–6,650	75
25.5	100	4,836	13,640	6,081a	16.3	5,813–6,347	78
29.6	100	5,488	14,896	7,114b	15.3	6,655–7,573	59
35.0	100	7,400	13,000	9,444c	15.7	8,790–10,098	18
Field-simulated	100	4,505	15,626	5,637a	22.3	5,360–5,913	85

Values with common letters were not significantly different at $P \leq 0.05$. (Fisher LSD multiple comparison test).

Table 3. Physiological development time in degree-hours centigrade (°h) at constant or field-simulated temperatures for summer form codling moth pupae in Yakima, WA

Temp. °C	No. pupae	Min. no. °h	Max. no. °h	Mean no. °h	Mean no. days	95% CL	% emerged
Constant							
14.8	62	4,877	10,214	6,185bc	53.7	5,699–6,672	59.7
20.1	75	4,848	8,403	5,652b	23.3	5,505–5,796	85.3
25.5	78	3,472	16,492	5,639b	15.3	5,271–6,006	94.7
29.6	59	4,861	12,387	6,237c	13.5	5,961–6,705	100.0
35.0	18						0.0
Field-simulated	85	2,127	7,863	4,710a	26.7	4,562–4,858	93.2

Values with common letters were not significantly different at $P \leq 0.05$. (Fisher LSD multiple comparison test).

The x-intercept for pupae was at 10.7°C using the three lower temperature data that were linearly related (lack-of-fit $F = 0.24$; df = 1, 174; $P \leq 0.05$) (Fig. 1C). When the 29.6°C data were included the data were not linear ($F = 16.7$; df = 2, 230; $P \geq 0.05$) where the x-intercept was at 9.2°C. The 35.0°C temperature was lethal.

Thermal units were determined using base temperatures of 7, 10, and 13°C to illustrate how much error there can be using an incorrect base temperature (Fig. 2 A and B). Thermal units were similar at each of the six (eggs) or four (larval–pupal) rearing temperatures used, giving a nearly horizontal regression line (Fig. 2 A and B) only at base temperature 10°C. At base temperature 7 or 13°C the number of thermal units were not similar at each rearing temperature giving a negative or positive sloped regression line, a clear indication that the base temperature was incorrect.

Discussion

Egg Development. The physiological development time (degree-hours centigrade) for eggs in this study, with 10°C as the base temperature, was 2,100 ± 87 degree-hours, and was comparable to the values obtained by Glenn (1922), Wyniger (1956), Glen and Brain (1982), and Richardson et al. (1982), but it was 300 degree-hours lower than Cranham's (1980). Based on these reports, egg development time, in degree-hours centigrade, seems to be geographically consistent, because the cited studies represent divers geographic regions. Common development time may have a genetic basis because codling moth, at all localities worldwide, probably had their origin in Europe, with one exception, South Africa (Pashley and

Table 4. Physiological development times in degree-hours centigrade (°h C) at constant or field-simulated temperatures for male or female codling moth larvae-pupae in Yakima, WA

Temp. °C	Development time °h C	
	Male	Female
Constant		
14.8	12,406a	13,073a
20.1	11,491a	11,960a
25.5	11,439a	11,053a
29.6	13,326a	14,032a
Field-simulated	9,955b	10,002b

Mean development time for males and females at constant temperatures was not significantly different at $P \leq 0.05$. (Fisher LSD multiple comparison test) or at field-simulated temperatures. But mean development time was significantly shorter at field-simulated temperatures.

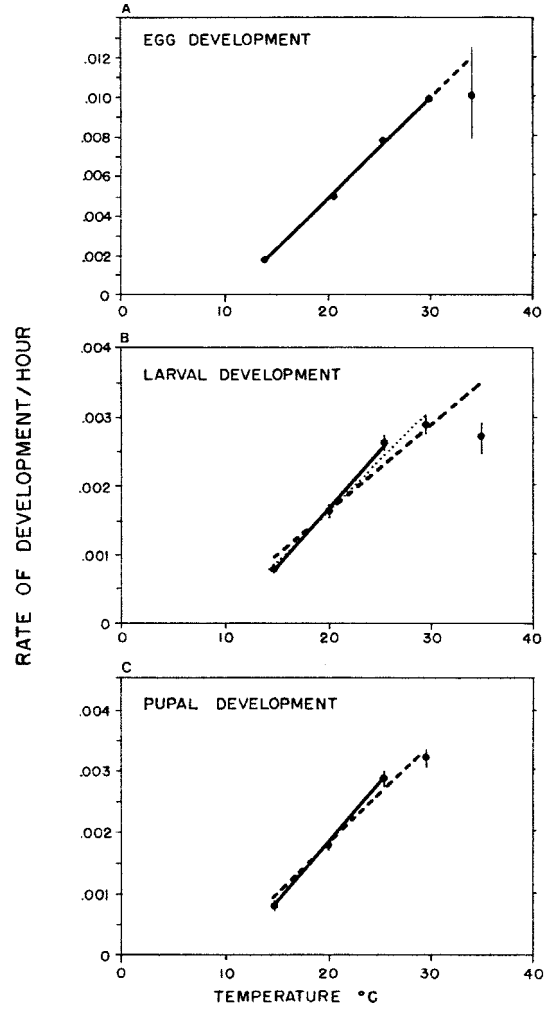

Fig. 1. Development rate of codling moth as a function of temperature. (A) Eggs using four (—) or five (- -) temperatures. (B) Larvae using three (—), four (· · ·), or five (- -) temperatures. (C) Pupae using three (—) or four (- -) temperatures. Vertical bars represent the 95% CL.

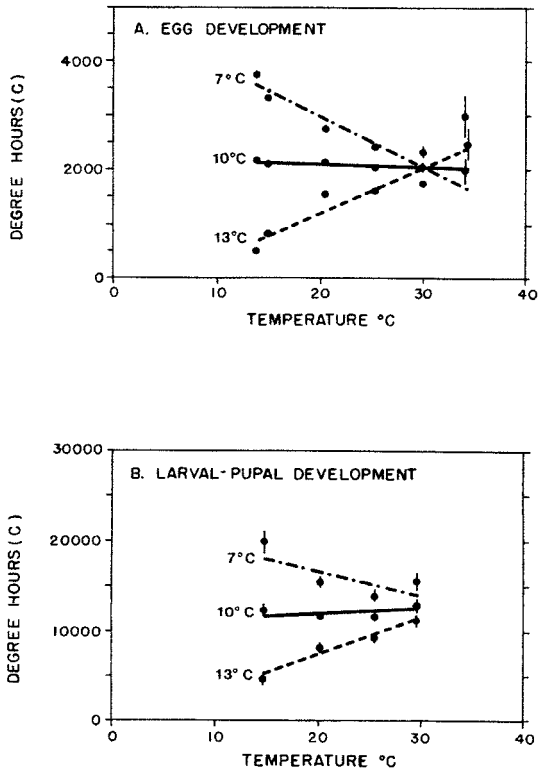

Fig. 2. Development time of codling moth as a function of thermal unit accumulation. (A) Eggs using six temperatures at base temperatures of 7°C (·—·), 10°C (—), or 13°C (– –). (B) Larval–pupal using four temperatures at base (b) temperature 7, 10, or 13°C, as in A. Vertical bars represent the 95% CL. The *x*-axis denotes the temperatures at which the different stages were reared.

Bush 1979). Egg development time (range, 1,600–2,430 degree-hours) was short compared with larval and pupal development time (range, 3,470–16,492 degree-hours). The egg is a selfcontained unit and needs only heat for development. Its narrow range of development time and consistency makes the egg an excellent stage to use for a phenology model to time control techniques. Applying the first cover spray at first egg-hatch (i.e., 2,000 degree-hours after biofix) gave improved control versus using the CODMOTH model (Brunner et al. 1982, Anonymous 1985).

Larval Development. Larval growth rate was retarded when reared at constant temperatures ≥29.2°C (Table 2). Growth rate was not retarded using naturally occurring field-simulated temperatures, even when segments of the daily temperature exceeded 34°C. Shorter development time at field-simulated temperatures is not unusual. Hagstrum and Hagstrum (1970) listed 48 insect species whose rates of development were increased when reared at field-simulated temperatures as compared with constant temperatures. Taylor and Shields (1990) also listed several species that had accelerated development at field-simulated versus constant temperature. Most phenology models have been constructed from data (particularly the low and high temperature thresholds) derived from development data of insects reared at constant temperatures (e.g., see VanKirk and Aliniazee 1981, Rock and Shaffer 1983, Regniere 1984). These models frequently overestimate the development time. For example, codling moth larval development time would be overestimated by ≈551 degree-hours, pupal development by 1,115 degree-hours—a difference of from 1.1 to 11.5 d for larvae, 2.3 to 23.2 d for pupae, depending on temperature conditions.

Fifteen percent of the larvae reared at 14.8°C under long-day (17:7 [L:D] h) conditions entered diapause, but there was no diapause at higher rearing temperatures. Low temperature of long duration (up to 103 d) apparently induced diapause, even under long-day conditions. This was a significant finding regarding diapause and was not previously reported. Temperature does interact with photoperiod; cool temperatures shorten and high temperatures lengthen the critical photoperiod for codling moth (Garcia-Salazar 1984). How low temperatures alter the critical photoperiod has not been investigated, but some work has been done on the effect of high temperature. High temperature (30°C) and very short development time (20 d) overrode short-day (8:16 [L:D] h) conditions to prevent diapause (Brown 1985). In the Yakima River basin from 10 to 20% of the indigenous larvae entered diapause in the spring (vernal diapause) during that time of year when daylength is approaching its maximum (J.F.H., unpublished data). Low temperature and slow growth rates may be the mechanism responsible for vernal diapause. However, further studies are needed to verify our hypothesis regarding vernal diapause.

Pupal Development. Minimum and maximum development times were more variable for pupae than for larvae. Pupae did not survive at 35.0°C, whereas a few eggs and larvae did survive. Pupae had a development time of 4,710 degree-hours at field–simulated temperatures, which was significantly shorter than 5,637 degree-hours at constant temperature. Apparently, pupae were more temperature sensitive than either eggs or larvae. Pupae seemed to be more responsive to field-simulated temperatures than larvae. Pupae developed almost twice as fast at field-simulated temperatures, as larvae (927 versus 551 degree-hours).

Total Development. Field-simulated temperatures were more favorable for codling moth development than were constant temperatures. Although development rates between constant and field-simulated temperatures were not significant in either the egg and larval stages, they were significantly shorter at field-simulated temperatures in the pupal stage. When combining the larval and pupal development times, the developmental rates for field-simulated temperatures were significantly shorter than at constant temperatures, by ≈1,500° h. That is 6 d shorter at 20°C and 12 d shorter at 15°C.

Base Temperature Determinations. Extrapolating the regression line to the *x*-intercept to determine the

base temperature applies only to linear portion of the sigmoid curve. In particular the curves are nonlinear at low and high temperatures (Wagner et al. 1984). Then it becomes a question of whether any of the points off the linear line should be included to determine the *x*-intercept. For codling moth larvae, as illustrated in Fig. 1B, it was possible to derive three *x*-intercepts, 6.9, 9.3, and 10.3°C, depending on how many points that deviated from linearity were used in the calculation. The base temperature for codling moth has been reported to be as low as 8.0 or as high as 11.1°C (Falcon and Pickel 1976, Falcon et al. 1976, Shaffer and Gold 1985). Rock and Shaffer (1983) used five temperatures to calculate the *x*-intercept (9.9°C) even though the data were significantly nonlinear. Unfortunately, the *x*-intercept does not confidently identify the base temperature (VanKirk and Aliniazee 1981, Hawthorne et al. 1988), and if the base temperature was inaccurate that would introduce too much error into the growth rate equation. A method is needed whereby one can verify the accuracy of base temperature when determined using the *x*-intercept.

The same data used to determine the *x*-intercept can be used to determine the thermal units. Theoretically, the number of thermal units at each temperature will be the same (a constant), provided the base temperature (b) was correct. If b was too high, the number of thermal units will increase as the rearing temperature (t_i) increases, the opposite if the base temperature was too low, as the example in Fig. 2 illustrates (Hoover 1955, Arnold 1959). If the thermal units lack a horizontal fit, then other values for b may be substituted to test for a better fit.

The base temperature may also be determined using the thermal unit test, rather than just using it to verify the accuracy of the *x*-intercept. Using temperature integrators, in the field or in the laboratory, the actual number of degree-hours for the development of any growth stage is readily determined, and is more accurate than using thermostat settings with their inherent on-off temperature differentials.

To use the thermal unit fitness test it was necessary to determine development time d_i for a series of temperatures, t_i, e.g., at five degree intervals. We began the temperature series at a low temperature, because the differences in thermal unit, if b is incorrect, will be more pronounced when the development time was longer. When d_i has been determined, one can substitute any logical value for b and calculate the thermal unit using equation 1. With the correct b, thermal units should be similar at each temperature point within the range for normal development. Pruess (1983) found that for most insects b was between 5 and 15°C. If b is too high, thermal units will have a positive slope, i.e., the thermal unit will increase as t_i increases; if too low the thermal unit will have a negative slope, i.e., the thermal unit will decrease as t_i increases. With the correct b, the thermal unit will be similar at each temperature, i.e., when data points are connected the line formed will be horizontal (Fig. 2). By substituting b values into equation 1, the b giving the best fit is easily determined.

For codling moth, with $b = 10$°C, the thermal unit number was a constant for egg, larval, and pupal development, except at near lethal high temperatures. Unquestionably, field-simulated temperature regimes were more favorable for development than constant temperatures. Therefore, to improve our phenology models they must be based on development rates at field or field-simulated temperatures, not on rates determined in the laboratory at constant temperatures. At constant temperatures there is a strong likelihood that artifacts are being introduced into the model.

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